SEXUAL SELECTION AND TERRITORY SIZE IN MALE CUNNERS, TAUTOGOLABRUS ADSPERSUS, IN CONCEPTION BAY, NEWFOUNDLAND

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SEXUAL SELECTION AND TERRITORY SIZE IN MALE CUNNERS, *Tautogolabrus adspersus*, IN CONCEPTION BAY, NEWFOUNDLAND

by

© Guy Martel

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of the requirements for the degree of
Master of Science

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ABSTRACT

The occurrence of sexual selection was investigated in the cunner, Tautogolabrus adspersus (Walbaum), in Conception Bay, Newfoundland. Field observations show that the number of spawns was different between territorial males and, consequently, that sexual selection occurs among those males. Correlations between spawning success and physical and behavioral characteristics of territorial males indicate that the females tend to base their choice on male's characteristics rather than on those of the territories.

However, the ultimate goal of territoriality appears to be related to reproduction and, since territorial males spend most of their active time on their territories, a proximate goal is maintenance. Differences exist between sizes of males' territories, and factors which could affect the size of those territories were investigated. Geophysical differences (influencing the defendability of territories) and food quantity and distribution inside territories are responsible for most of the variation between territory sizes. The occurrence of a previously undescribed type of behavior in the cunner, termed 'peregrination', is described.

ACKNOWLEDGEMENTS

In any study involving SCUBA diving, field assistance is mandatory. Nevertheless, I wish to particularly thank Elizabeth Kingsland and Ian Roy for their assistance (and sometimes their patience). Other persons who helped with the diving were Kevin Pauley, Kent Gilkinson, Pierre Ryan, Norah Davidson, Scott Wilson, David Methven, Glen Gilbert, Ben Davis, Peter Noble, Steve Dawson and John Lawson. To all of the preceding, my most sincere thanks. Robert Hoopef offered considerable (and valuable) advice and material support in diving matters. Photographic work was expertly done by Mr Roy Ficken, who often went beyond my requests. Memorial University's Machine Shop staff (Technical Services) almost performed miracles in creating reliable instruments from hazy sketches. Their enthusiasm is vividly remembered. This work would not be in its actual form without the help, advice and, I must admit, great patience of all the staff of Memorial University Computer Services. Mr C. McNamara kindly gave me the authorization to use ETV's printer on which these pages are printed. I am also indebted to Dr R. Hollett who acted as if he enjoyed correcting several drafts of the thesis and in doing so,

considerably reduced the damages I was inflicting upon the English language.

This thesis benefited appreciably from discusssions with Robert Pottle, Joe Brown and Derek Keats. Statistical advice was kindly provided by Drs B. Kim and R. Jain, and especially by Mr Bruce Gellately, whose help in the matter was invaluable. Drs D.H. Steele and G.R.South read and criticized the manuscript. During all the aspects of this work, I was repeatedly reminded of the positive influence of my advisor, Dr John M. Green, whose support was much more than financial. Some people say that money can't buy happiness, but as any student will tell you, the cost of happiness has considerably gone up recently anyway. In that regard, financial support was provided by a fellowship from the Department of Graduate Studies and by an operating grant to Dr J. M. Green from the National Research Council of Canada. Finally, I will always be deeply indebted to Dr J. H. Himmelman, without whom I probably would never have come to Newfoundland in the first place.

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INTRODUCTION

Sexual reproduction, as opposed to asexual reproduction, is the dominant form of reproduction among the higher vertebrates such as fishes, reptiles, birds and mammals (Daly and Wilson, 1978).

The prerequisites to successful sexual reproduction are numerous (in fact so numerous that some authors have wondered why animals bother to use sexual reproduction at all - Maynard Smith, 1971; Williams, 1975; Barash, 1976) : first the potential mates must be in physical proximity. Then, they must be able to recognize each other and to evaluate their partner's reproductive state in order to avoid time and energy losses. To assess a mate, an animal can receive and convey information via several modes, e.g. chemical, olfactory, visual, tactile, auditory (Wilson,

1981). In some species, reproduction involves complex behavioral sequences, such as in fishes and birds (Alcock,1979 ; Wilson, 1981) .

Because individuals resulting from sexual reproduction are different from each other, an animal is often confronted with some choice. When one sex represents or possesses a limited resource, that sex is often competed for by the other and can usually choose its mate. Because one sex 'selects' the other, this process is generally referred to as sexual selection.

The selecting sex has to find a way to evaluate the quality of its mate : this quality can be appraised directly by looking at the mate or indirectly by looking at its 'feats' or 'possessions', e.g. size and quality of territory, quantity and quality of food offerings, etc.. In the former case, where the mate is directly evaluated, this often leads to mating systems where males (generally the evaluated sex) compete directly against each other on a common breeding ground, such as leks (Wilson, 1981).

The indirect evaluation often leads to territoriality, the mate whose territory is the best mating with the most or the best individual(s) of the other sex. The problem lies in finding what the 'best' is according to each species.

Sexual selection has been investigated in many vertebrates including fishes (see Ralls, 1977; Robertson and Hoffman, 1977; Keenleyside, 1979 ; Wilson, 1981). Among fishes, females apparently show much variation in their selection criteria. For example, in the California reef fish, Embiotoca jacksoni, the territory site and its shelter quality rather than the occupant apparently influence the female choice (Hixon, 1981). For the bicolor damselfish, Eupomacentrus partitus, also a territorial species, male characteristics have precedence over those of the territory in influencing female choice (Schmale, 1981). Downhower and Brown (1980) found that size (size being positively correlated with parental care in this case) of territorial males was the main determinant of female choice in Cottus bairdi, the mottled sculpin.

The above examples involve fish species displaying territoriality, which is defined by Wilson (1981) as the more or less exclusive occupation of an area by an animal or a group of animals through overt defense or advertisement. Territorial species make good subjects for studies on sexual selection because the territorial individuals stay within a more or less constant and well delimited perimeter for generally long periods of time . In the case of fishes, these individuals can be tagged and followed and measures of

reproductive success and behavioral or physical parameters can be made and compared.

The cunner, Tautogolabrus adspersus, is a fish species which lends itself well to a study of sexual selection. Its territorial behavior in Conception Bay, Newfoundland, has been described by Pottle and Green (1979b) and other aspects of its behavior quantified. Some adult males actively defend territories (varying from 20 m^2 to 100 m^2 in area) from which they exclude other males, juveniles and occasionally other species. They hold these territories for their entire period of activity, although they seem to decrease their vigilance a few weeks before entering the dormant state.

The males have been observed to keep roughly the same territories from year to year (Pottle and Green, 1979 b). If a territory owner is removed, he is either replaced by a new male, which tends to point to the existence of a floating population, or adjacent neighbours extend their territories into the vacant one (Pottle, 1978).

Territorial cunners also show strong homing behavior, being able to home after displacements of at least 4 km and after having been kept in aquaria for 9 months (Green, 1975). Territoriality seems to occur to a lesser extent among

females (Pottle and Green, 1979b) : some of them have been observed to defend portions of males's territories against other females. Their aggressive displays towards resident males are generally ignored .

The territorial cunners tend to distribute their activities differentially in time : feeding is more frequent in the morning (Martin, 1979) while patrolling is of greater occurrence in the afternoon (Pottle and Green 1979b).

Territorial behavior is frequently found throughout the animal kingdom (Wilson, 1981). In fishes, it is present in many substrate-bound species and is related to the protection of a limited resource : shelter, food or breeding site (Keenleyside, 1979). Whenever these resources are scarce and defendable, one might expect to find territorial individuals, which, in most fish species, are males (Blumer, 1979).

Male cunners have been observed to display territoriality but the resources they defend have not been fully ascertained. Pottle and Green (1979 a,b) found that the territories of cunners studied in Conception Bay were of different sizes, and that this was not related to the owner's length (or size). Pottle (1978) also concluded that the

primary function of territorial behavior in cunners was the " defense of spawning area from which potential rivals are excluded " . But Pottle and Green (1979b:2345) also remarked, " We have no data on the relative 'quality' of territories, with regard to abundance of benthic prey. "

Olla et al. (1981) manipulated the food supplies of territorial tautogs (Tautoga onitis), a close relative of the cunner, under laboratory conditions and concluded that food density played an important role in the tautog's territorial behavior and hypothesized the same for the cunner.

Territoriality in male cunners might be a function of sexual selection by females. It is known that there is competition for the acquisition of territories and that territorial males spawn more often than non-territorial ones (Pottle and Green, 1979b). Territorial male cunners do not generally restrict female cunners movements and moreover tend to compete among themselves to gain access to these females (Pottle and Green, 1979a). However, their spawning success has not yet been investigated. Whether it is uniform (all territorial males spawning approximately the same number of times during a spawning season) or not would

be a good indicator of the presence (or absence) of sexual selection in this species.

Consequently, the major purpose of this field study was to determine if differential spawning success (*) exists among territorial males and if so, to find out on what the female cunner bases her choice : the territory or the male himself. Another goal was to try to find which physical and/or biological parameter(s) most influence the size of a cunner's territory.

(*) Spawning success is here defined as the number of spawns observed in a given period of time.

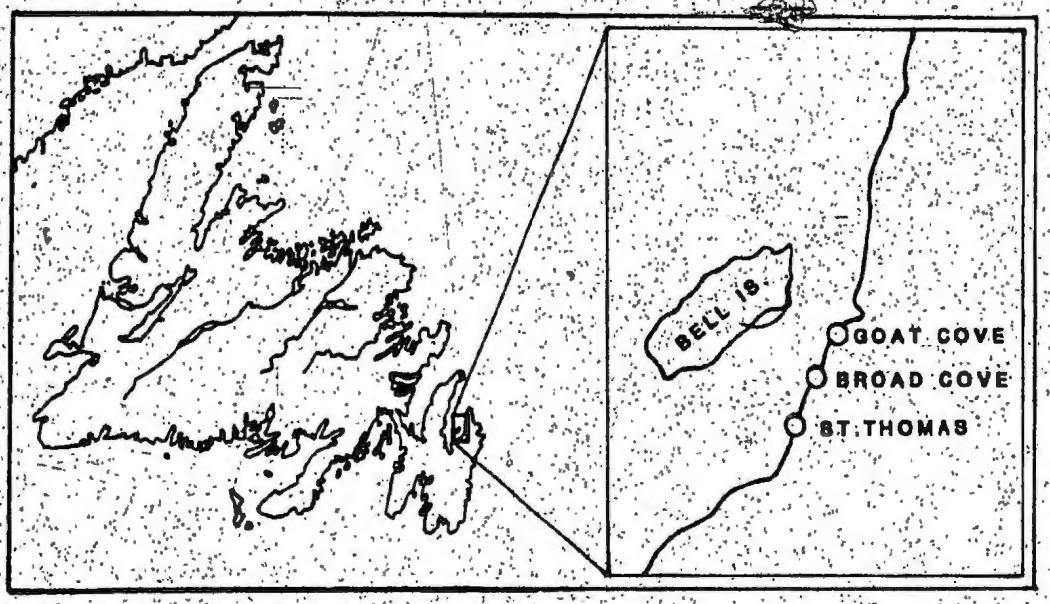
MATERIALS AND METHODS

Study sites

All behavioral data were collected *in situ* in Broad Cove, Conception Bay, Newfoundland (lat.47 35.5′ N, long. 52 53.5′ W), subsequently referred to as the main study site (Fig.1).

The underwater topography of the site consisted generally of boulders, bare for the most part, over a rocky substrate. Sandy-patches began at a depth of about 10 m. The slope was approximately 10° seaward with a vertical drop-off of 3-5 m in the middle of the area.

Figure 1. Main collection and study sites.


BELL IS.
GOAT COVE
BROAD COVE
ST. THOMAS

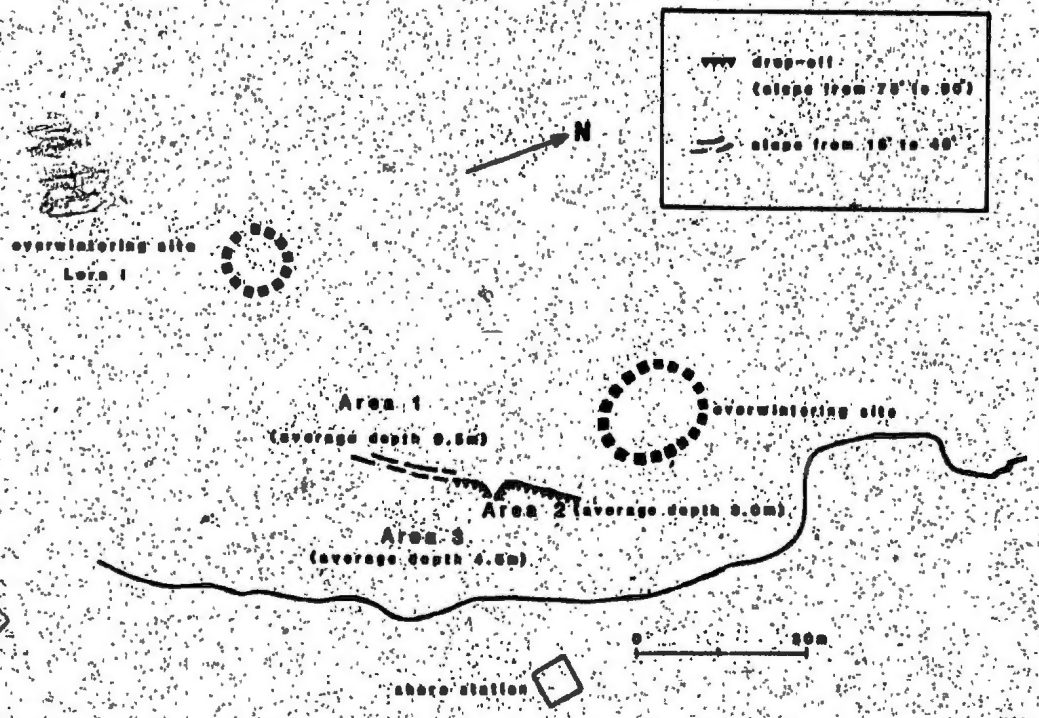
The depth ranged from 2.5 to 10 m, the shallowest part being just before the drop-off (Fig. 2). Territorial males were present throughout the general area and many of them were tagged from a previous study (Pottle and Green, 1979 a,b).

Behavioral observations

One of the goals of this study was to determine the correlates of female choice among territorial males. One way to achieve this is to find out if there is any differential spawning success between territorial males. The differences, if they exist, could then be linked to either behavioral or physical parameters.

In order to investigate the behavioral parameters, most of the fish, i.e. those in relatively shallow water, were observed by snorkeling. Those inhabiting deeper regions of the study site were observed by SCUBA diving. For the former, the observer floated on the surface over the fish, which did not seem to be disturbed by his presence (Pottle

Figure 2. Study site in Broad Cove.


drop-off
(slope from 75° to 90°)
slope from 15° to 40°
N
overwintering site
Lure 1
Area 1
(average depth 0.5m)
overwintering site
Area 2 (average depth 3.0m)
Area 3
(average depth 4.0m)
0
500
shore station

and Green, 1979 a,b). During underwater observations, great care was taken to stay immobile and as high in the water column as the visibility permitted.

Observations were recorded either on waterproof paper or, as for most of the 1981 observations, with specially designed water proof event-recorders constructed by Memorial's Department of Technical Services. These consisted of eight pocket calculators transformed to act as counters and enclosed in water-tight plexiglass boxes on which notes could be written (Fig. 3). Each counter was activated by pushing an external button. A clock (timer) was enclosed in each event-recorder.

In the spring of 1980, seven males were selected on the basis of their ease of identification (visibility of tags, mainly). Three others were captured in deeper water beyond the drop-off and tagged. The number of males observed per day varied from eight to ten, depending on the number of divers available. In 1981, eight males were again selected for observation, among which six had been studied the previous year. They were followed through the entire spawning season.

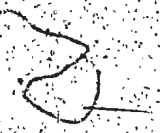
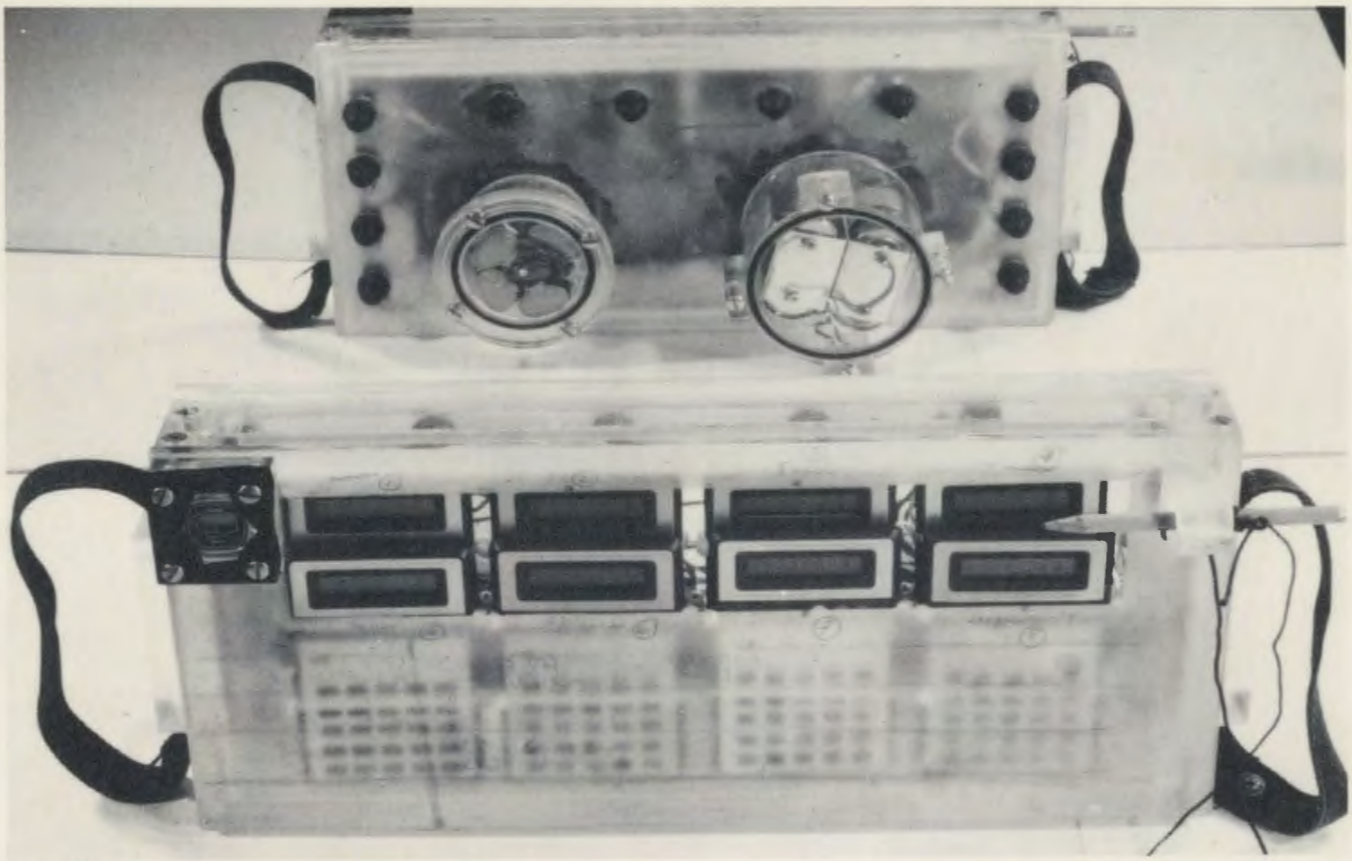


Figure 3. Event recorder of the type used to collect behavioral observations.



During each observational period, a territorial male was observed for thirty min. and his behaviors were recorded. A brief description of each of the behaviors recorded follows (for more details, refer to Pottle and Green,1979b) :

approach : Forward movement by one fish towards another following an interception course.

chase : Quick movement by one fish following (chasing) another. Usually involves two fish .

lateral display : Two fish present a flank to one another and swim slowly, following a parallel course, often reversing direction, the mean distance between the two fish being 25-75 cm (Pottle and Green 1979).

frontal display : Two fish face one another at close distance. The pectoral fins beat at low amplitude. Gaping is commonly observed.

gape : The lips are protruded and the teeth are exposed . This display was mainly observed as part of the frontal display.

bite : The fish quickly closes its jaws on another fish . Can follow a gape or a frontal display, but also seen performed upon other species.

melee : Quick sequence of postures and actions in which two fish strike at each other. It is initiated most of the time by frontal display and gaping.

courtship : A male swims in an arch, the highest point of which is 1-1.5 m above the female, with his head turned sharply in her direction and his dorsal fin erected .The male swims in a carangiform (*) mode while the female stays nearly immobile or swims slowly.

(*) carangiform swimming : type of locomotion in which a fish moves forward by sweeps of the tail region. For more details, refer to Keenleyside (1979).

feeding behavior : A fish plucks quickly at an object, his lips protruded. Feeding was seen to take place on the benthos or in the water column. When on the benthos, the fish was assuming a head down, nearly vertical posture.

Territorial males tend to distribute their activities differentially in time (Martin, 1979; Potttle and Green, 1979b). In 1980, observations were made during the morning and afternoon of each day of sampling to quantify the differences between morning and afternoon. This accounted for 551 dives in 26 days.

In 1981, the only behaviors quantified were those related to or occurring at the same time as territorial defense and reproductive behaviors. Consequently, observations were conducted only in the afternoon, necessitating 144 individual dives in 18 days.

Capture and tagging

The territorial males studied in Broad Cove were captured by entanglement in a 25 mm mesh net during both summers, at irregular intervals. This was done to facilitate their identification and also to reduce the potential drag caused by algal growth on their tags. After capture each fish had its tag cleaned of algae, its length measured and, in some cases, its weight measured on a triple beam balance. The success of capture varied, depending upon the type of habitat a fish was patrolling and apparently whether or not the gill net had been used in the area before, since males soon came to avoid the gill net on their territory. One fish escaped all capture attempts for the 2 years of the study.

The tags used were Floy FD 67 'spaghetti' tags coupled with Carlin tag ends. Most of these tags lasted throughout the two years. Each was either color coded, numbered, or both.

Morphometric data

Some cunners were measured and weighed in order to provide growth data. Part of these measurements came from data collected in previous years .

The non-territorial males had been captured in July, 1979, and August, 1978, while the females had been caught in August, 1978 and 1979, all with the use of baited hoop nets. Because of their reluctance to leave their territory or to join feeding aggregations, territorial males were speared . This was done in July and August, 1979, and in August 1981.

To provide data for weight and length over a three month period, 54 fish were caught on the study site on November 10th and 19th, 1981, with the use of gill nets . Of this number 28 were male (presumably non-territorial) and 26 were female . Sexing was done by examination of the gonads.

Territorial males from the same area were caught at about the same time. However, these fish were not kept but were released in order to provide further data for future experiments.

Mapping of male territories

The territories were marked with red painted rocks around the beginning of August (*) of each summer. Territorial limits were most often rendered apparent by the number of lateral, frontal and gape displays which were taking place on specific spots. After 2 months of observations, most of the territorial boundaries were thus known and almost all rocks were placed in one day, at points where territorial disputes were frequent. Some boundaries were subsequently readjusted according to further

(*) The choice of this time of year is related to logistics, not to any cycle. Undisturbed territorial males have been observed to keep the same territory site (and size) throughout the season and even, in some cases, from year to year.

observations. The distances between markers were directly measured and the area of each territory was calculated through triangulation.

Alimentary tracts(*) content analysis

(*)Note: The cunner does not possess a stomach as such, but rather an elongated alimentary tract and a three limbed and S-looped intestine (Chao, 1973).

A common reason to defend a territory is because it represents a valuable food source (Wilson, 1981). Since territorial cunners spend most of their active time within the same area, they have to obtain their nutritional requirements from it. One of the objectives of this study was to evaluate physical parameters by which territories might differ and food content is one of them. This was done in two steps : first, alimentary tracts contents of territorial males were analysed, and second, samples of the

substrate in different territories were taken and analysed (cf Benthic Samples, this section). The first step was done to determine if some food items are preferentially eaten.

From July to August, 1981, 38 territorial males were collected from Goat Cove and areas around St.Thomas (Fig. 1, p.9). Preliminary surveys had shown that except for the slope, which was slightly steeper (25° in the St.Thomas and Goat Cove areas vs 10° in Broad Cove), the substrate and topography of these sites were similar to Broad Cove. All the fish were taken between 11:30 and 13:00 to maximize the chances of obtaining specimens with full alimentary tracts (Pottle and Green, 1979 a). The fish were identified as territorial after 10 to 15 min. of observation for each and then harpooned with 'Hawaiian slings'. Following capture, a fish was immediately brought back to a boat where it was killed and its alimentary tract injected with 10% formalin. All the fish were subsequently kept in 10% formalin.

The content of each alimentary tract was identified to the lowest possible taxon and the items were measured to the nearest millimeter when possible. Most of the food items were preserved in 70% alcohol.

Benthic samples

After individual territories had been mapped, they were sampled in order to determine the abundance of food items.

During May and June, 1980, a preliminary sampling of the distribution and abundance of potential food organisms of the general area was done : 48 samples were collected and analysed. This sampling was preliminary in that neither the territorial boundaries nor the territorial males were known at the time. Also, methods of sampling were subsequently refined.

Proportional sampling of specific territories was done as follows : a certain number of quadrats was agreed upon (to determine this number, the average time to be spent underwater per quadrat was taken into account) and the number of quadrats was allotted proportionally to the area of each territory. Thus, the following equation was used :

$$n(i) = N \times \frac{a(i)}{A}$$

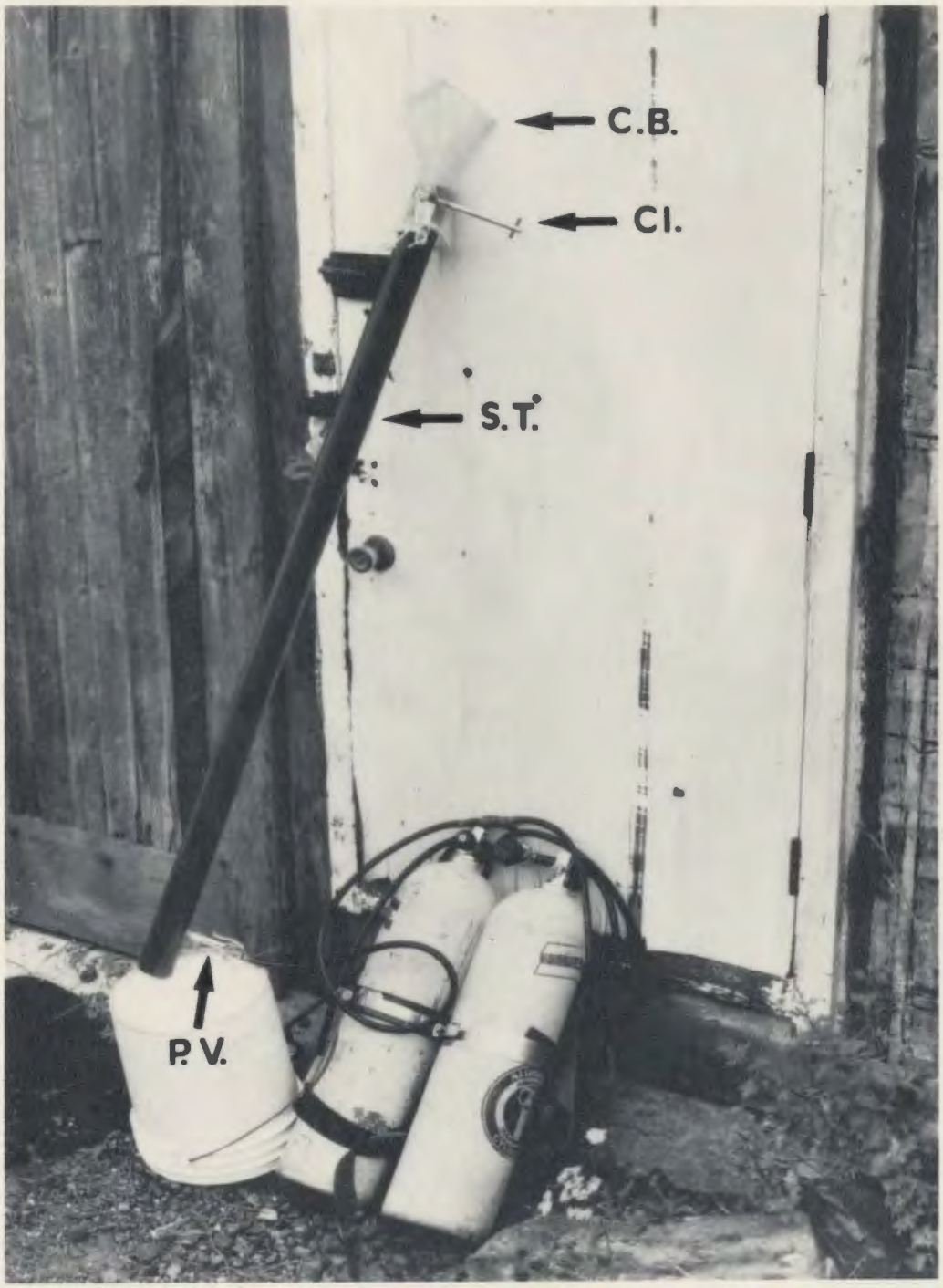
where $n(i)$ = number of samples to be taken in ith territory

N = total number of samples

$a(i)$ = area (in m^2) of ith territory

$A = \Sigma\, a(i)$

Figure 4. Air dredge of the type used to collect benthic samples in territorial cunners' territories. S.T.: suction tube, C.B.: collecting bag, Cl.: clamp, P.V.: pressure valve.


C.B.
CI.
S.T.
P.V.

The samples were taken with an air dredge consisting of a 1.5 m long plastic pipe, at one end of which was a pressure valve linked to double SCUBA tanks. The air, which could be released at will by the operator, created a suction effect while ascending through the tube. At the other end of the cylinder was a bag made of plankton net (mesh size = 0.5mm) attached by a modified clamp (Fig. 4).

Quadrats (0.25 m X 0.25 m) were randomly dropped on the territory to be sampled. Two divers then proceeded as follows: one noted the general description of the quadrat locus and its immediate surroundings, such as the percentage coverage of different algae, type of substrate, slope, etc., while the other collected the larger invertebrates by hand. One diver then scraped small invertebrates off the rocks and substrate inside the quadrat while the other aspirated them with the air dredge. Bedrock was cleaned bare while sandy substrates were sampled to a depth of approximately 0.4 m within each quadrat.

In September and October, 1980, six territories were sampled. Fifty five samples were partitioned proportionally in those territories. In October, 1981, three additional territories were sampled, necessitating

twenty three samples, the proportion of samples per territory being the same than in 1980.

When possible, all the invertebrates from the samples were identified to species and measured to the nearest mm. Afterwards, they were grouped into more general taxa to facilitate interpretation of the data.

Descriptions of the areas

Another physical parameter which might be of importance in a female's choice of mate is the location of the male's territory (e.g. Jones, 1981). Some topographical features might be common to certain territories which could in turn influence mate choice. To test this, qualitative descriptions of the territories are helpful in determining if they can be thereafter classified into general geophysical areas.

At the beginning of September, 1980, qualitative descriptions of the areas were made. Two divers first swam

about three to five m over a territory, during which time they noted the relief and type of substrate. Then, they went closer to the bottom (less than one m), noting the relative abundance of organisms in their paths, randomly turning over small rocks and noting the relative occurrences of invertebrates . Notes were taken on waterproof paper and compared by the observers after the dive.

Food manipulations

Territory size can be related to food supply (Wilson, 1981 ; Davies, 1978). With some fish, territory size has been experimentally demonstrated to vary with food density (Slaney and Northcote, 1974; Syrop, 1974 ; Ebersole, 1980; Hixon, 1981).

If this is the case for the cunner, we might expect to observe an inverse relationship between territory size and food density (or availability), if the fish feeds throughout the whole territory and assuming that the territory provides most of the energy resources for territorial cunners.

To test this hypothesis experimentally, I decided to limit the access of territorial males, with the use of nets,

to only a part of the food resources of the territories. Since the fish were to be prevented access to food, one had to make sure that what was measured was the consequence of the net's presence (i.e. no food) rather than the effect(s) of the nets themselves.

Consequently, in mid-July, 1981, a section of 25 m^2 of substrate was covered with .62 mm mesh net in an area ~ 750 m south of the main study site where territorial males were present.

Frequent snorkeling observations, although at irregular intervals, were made throughout the rest of July and August to determine if the presence of the nets altered the behavior of nearby fish. Cunners did not avoid the netted area and were frequently observed directly over the net. No quantitative data were taken.

At the end of August, 1981, six regularly observed territories were chosen for inclusion in this experiment on the basis of their relative sizes. Seven 30-minutes morning observations were carried out on each male over 7 days. These observations were as grouped in time as possible, weather permitting.

On September 2 and 3, five nets were installed covering, respectively, 50% (for two territories), 75% (two territories) and 100% (one territory) of the areas of five territories. The 6th territory was left uncovered as a control. Following this, more 30 min. behavioral observations were made for nine days, spaced over a period of 16 days mainly because of weather conditions.

Quantitative data analysis

SAS (Statistical Analysis System Institute inc.,1979) programs were used for correlation, regressions, multiple regression analysis, analysis of variances and *a posteriori* tests, t-tests, and normality tests. In multiple regression analysis, five methods of stepping through variables were used : forward, backward, stepwise, minimum R and maximum R. The number and order of inclusion of variables incorporated in the model were most often the same for the forward methods, except for the stepwise one because of the significance level for entry defaults(.15 as compared to .5 for other methods). The minimum R method examined slightly more models. When the results stem from this statistic it

is mentioned. Otherwise the stepwise or the maximum R procedures are used.

To minimize heteroscedasticity, logarithmic transformation was used (Sokal and Rohlf, 1981). Some Duncan's multiple range tests could not be performed through statistical packages and were, therefore, calculated with the help of a desk calculator (Montgomery, 1976).

RESULTS

Behavioral observations

A. Correlations between behavioral and physical observations

The observations of males in both summers were combined in order to provide more significant correlations. Results from 18 days of observations are shown in Table 1. The 18 days of data of 1981 were used while 18 out of 26 days, around the same time of the year, were utilized from 1980.

Table 1. Behavioral and physical parameters measured on males Tautogolabrus adspersus in Conception Bay. Area 1 = deep territories, Area 2 = near the drop-off, Area 3 = nearest to shore. Refer to Table 3 for more detailed descriptions of the areas.

Male	Total length(mm)	Territory size(m2)	Spawns	Courtships	Feedings	Aggressions	Area(1)	Mean depth(m)
1	242	36.3	6	214	14	562	2	3.0
2	243	47.9	2	39	17	366	2	3.0
3	259	32.7	4	249	12	429	2	4.5
4	255	45.2	8	334	15	542	2	3.0
5	266	101.3	13	303	21	361	3	4.5
6	252	102.7	7	195	20	384	3	4.5
7	247	52.2	4	30	17	224	1	8.5
8	260	41.8	3	58	27	432	1	8.5
9	230	22.9	4	175	3	478	2	3.0
10	251	39.7	5	69	41	131	3	4.5
11	246	82.3	5	86	18	198	3	4.5
12	258	19.2	3	125	7	330	2	4.5
13	242	41.7	7	117	13	284	2	3.0
14	(2)	13.8	1	16	11	180	2	3.0
15	243	41.1	4	62	7	178	1	8.5
16	276	72.2	2	38	11	207	1	8.5

(1) Refer to Table 3 for descriptions of the areas.

(2) This fish could not be caught.

In four cases the same males appear for both years (#'s 1 and 13; 3 and 12; 6 and 11; 7 and 15). These were taken as separate individuals because of their separation in time. Whether or not their quantitative behaviors of former years can affect their behaviors of subsequent years could not be ascertained, but it is doubtful. The fusing of both years strengthened correlations which would otherwise have only been hinted at were the data left in two separate groups (see Appendix).

Correlations between physical and behavioral parameters are shown in Table 2. Even though a correlation between two variables only means that they vary together and are not expressed as a function of each other (Sokal and Rohlf, 1981), it is interesting to note the correlation between the number of spawns and territory area ($R=0.56$, $P<0.05$), which indicates that males with large territories tend to spawn more often than males with smaller territories. Because of the nature of the two variables, it is hard to imagine a reverse cause-effect relation. However, it should be noted that the correlation between these two variables could also indicate that they covary with a third variable, not measured.

Table 2. Pearson correlation coefficients (1) between behavioral and physical parameters of territorial males Tautogolabrus adspersus in Conception Bay. N = 16, except for the correlations involving total length, where N=15.

	# of spawns	Feeding frequency	Courtship frequency	Aggression frequency	Mean depth of territories	Total length of males
Territory size	0.56*	0.50*	0.25	-.004	0.34	0.38
# of spawns		0.26	0.80***	0.33	-0.13	-0.03
Feeding frequency			-0.07	-0.20	-0.17	-0.36
Courtship frequency				0.67**	-0.33	-0.008
Aggression frequency					-0.38	-0.09
Mean depth of territory						0.49

(1) Values are Log10(X+1) transformed.

* P<0.05, **P<0.01, ***P<0.001

Territory size also varies significantly with the number of feeding behaviors observed ($R = +0.50$, $P<0.05$), but not with depth or length. The most significant correlation obtained is the one between spawning frequency and courtship intensity ($R=0.80$, $P<0.001$).

B. Description of areas

Following qualitative description of most of the territories, three areas were apparent : a deep one, another one including the surroundings of the drop-off, and a third area nearer to shore. The main differences between these three areas are summarized in Table 3.

C. Anovas on depth and geographical areas

The territory sizes and the behavioral and physical characteristics of the territorial males were classified according to depth and area. Anovas run using depth as a classification variable were not significant. However, when

behavioral parameters are tested with the areas as grouping variable, the difference in distributions of territory size (m) and number of feedings is significant ($P<0.008$ and $P<0.06$ respectively; Table 4). A posteriori tests reveal that territory size and number of feedings are greater in area 3 than in 1 or 2 (Table 4).

D. Multiple regressions of behavioral and physical parameters on territory size and spawning success

Multiple regressions were done to see to what extent variation in territory size and number of spawns could be explained by physical or behavioral variations among territorial males.

These variations do not account for much of the variance between territories (Table 5). The number of feedings accounts for roughly 28% of the difference between territories, but it is probably the territory size which influences the number of feedings and not the opposite. That leaves the length (size) of resident males, which accounts for only 4% of the variance (territory size is not significantly correlated to males' total length: $R=0.38$;

Table 3. Descriptions of three main geographical areas used by territorial males *T. adspersus* in Conception Bay.

	Area 1	Area 2	Area 3
Geographical situation	deep territories, seaward of drop-off	surroundings of the drop-off	nearest to shore landward of the drop-off
Average depth	7.5 - 9.5 m	3 - 4.5 m	4.5 m
Slope	approx. 5 degrees	varied (0 to 90 degrees)	5 - 10 degrees
Bottom composition	cobbles and small boulders (approx. 0.3m3) over rocky substrate gradually becoming sand offshore.	large boulders (1.5m3 and more) on bedrock; many crevices.	boulders (0.5 to 1.5 m3) on bedrock.
Corralline (1) algae cover (2)	20 to 95 %	approx. 60 %	35 to 95 %
Overview	This is the deepest area. The bottom is relatively flat but offers many shelter sites for large cunners and for lobsters in what seems to be a network of small galeries under the coralline algae cover. The swell is almost never felt.	The shallowest area, often subjected to the swell. It provides the most numerous obstructions to horizontal visibility, there are many clumps of *Agarum cribosum* and of *Desmarestia* sp. and the area has many shelter sites for lobsters, eelpouts, etc., as well as for small cunners. This region has the most varied fauna and flora.	The relief of this area is generally flat with sparse boulders. Almost no shelter site. The non coralline vegetation is limited to a few thalli of *A. cribosum*.

(1) These include *Lithothamnion glaciale*, *Clathromorphum circonscriptum* and *Corallina officinalis*.

(2) The percentages stated represent the average of different estimations made by the observers. A few percentages calculated with grids surimposed on photographs revealed that these estimations were close to reality.

Table 4. Results of anovas testing the effect of geographical areas (cf. Table 1) on behavioral and physical parameters of territorial males T. adspersus in Conception Bay.

Variable	F	P>F	A posteriori test (Duncan's) (1)
Total length of male	1.00	0.40	N.S.
Territory size	7.30	0.008	3>2*, 1>2
Aggression frequency	2.08	0.16	N.S.
# of spawns	2.53	0.12	N.S.
Courtship frequency	2.17	0.15	N.S.
Feeding frequency	3.44	0.06	3>2*, 1>2

(1) Numbers refer to area

*P<0.05

Table 5. Stepwise regression of the variables (1) in Table 2 on territory size.

Variable entered(*)	Variance accounted for by variable(R2)	Total variance	Mean Square Error(MSE)	F (model)
Feeding frequency	0.28	0.28	0.033	4.97
Total length of males	0.04	0.32	0.034(a)	2.78
Aggression frequency	0.01	0.33	0.037	1.75
Mean depth of territories	0.001	0.33	0.040	1.20

(1) Values are Log10(X+1) transformed.
(*) Order of inclusion based on Minimum R2 improvement.
(a) The entry of this variable and of the following does not contribute significantly to the fit of the model.

n.s., Table 2). Obviously, some other variable(s) have to be measured to find a good predictor of territory size.

On the other hand, differences in number of spawns between males are best explained by the variation in the number of courtships (52%) and in territory size (17%) which together account for 69% of the observed variance (Table 6).

Territorial behavior

A. Onset

During the two years of observations, cunners emerged from the substrate around the middle of May and formed dense aggregations for about two weeks. One of these aggregations was 25 m out from the drop-off and another one was over what had been the site of the Lora I underwater habitat (cf. Green, 1975) (Fig. 2, p.11). The density of fish remained high in those areas throughout the active months.

Territorial males began to arrive on their territories

Table 6. Stepwise regression of the variables (1) in Table 2 on spawning success.

Variable entered(*)	Variance accounted for by variable(R2)	Total variance	Mean Square Error(MSE)	F (model)
Courtship frequency	0.520	0.52	0.017	13.95
Territory size	0.170	0.69	0.012	13.33
Aggression frequency	0.050	0.74	0.011	10.55
Total length of males	0.041	0.78	0.010	9.05
Feeding intensity	0.035	0.82	0.009	8.13
Mean depth of territories	0.010	0.83	0.10(a)	6.49

(1) Values are Log10(X+1) transformed.

(*) Order of inclusion based on Minimum R2 improvement.

(a) The entry of this variable and of the following does not contribute significantly to the fit of the model.

shortly after formation of the large groups, presumably coming from there. Cunners did not feed for two-three weeks after emergence, as evidenced by their lack of response to food (i.e. crushed sea urchins) until the water temperature had risen to about 6°C. Aggressive interactions began to be frequent around mid-June when water temperature rose to 10°C and they lasted until the fish became inactive.

B. Peregrinations

After the spawning season was over, some males began to wander occasionally from their territories. This became more frequent as water temperature decreased.

Those excursions all followed the same pattern : a male suddenly left his territory, swimming in steady labriform (*) movements. The course was as straight as the relief permitted and seemingly without hesitation. Males usually travelled 2-3 m above the substrate and headed to one of the two aggregations. Males leaving area 1 generally

(*) labriform locomotion : type of swimming in which a fish uses mainly its pectoral fins. For more details on this subject, refer to Keenleyside, 1979.

went to the Lora I group, although in one instance one went to the group off the drop-off. Males leaving areas 2 and 3 also went to this latter site .

These males were often chased by residents of territories they crossed. In all observed instances the intruder fled. No social display was noted during their stay in the group. Males usually remained in the aggregation for less than two minutes and were generally out of their territory for less than seven minutes.

C. Intra- and inter- specific territorial behavior

Territorial behaviors such as chases, lateral displays, etc., were observed more frequently in the afternoon than in the morning. Adult males were regularly chased, both morning and afternoon, while females were shown more hostility in the morning than in the afternoon. Juveniles, when present, were chased in almost all cases (cf. 'Juveniles', next section).

Other species were rarely chased. The few observed chases were of winter flounders (Pseudopleuronectes sp) or

rock gunnels (Pholis gunnelus). Eelpouts (Macrozoarces sp), lobsters (Homarus americanus), capelin (Mallotus villosus) and small cod (Gadus sp) were left undisturbed when present.

Reproductive behavior

A. Females

Females normally moved from the group off the drop-off to the territories around 14:00-15:00 h and thus initiated courtships from resident males. Although most of females came from that aggregation, some were already present on the territories. Whether they were territorial or not, as described by Pottle and Green (1979b), was not determined.

Male response to females varied : some males performed only courtships while others equally courted and chased the other sex. Although some ophiuroids were in two instances snatched from females by resident males, chasing was not

generally associated with female feeding behavior, at least not in the afternoon.

Courtship usually elicited flight or no response at all from females. A receptive female would stay still until the courting male was above her and performing wigwag movements. Spawning rush followed soon afterwards, at the apex of which gametes were released. In the great majority of spawns observed, the male described a strong arch around the female while descending. A courtship sequence was likely to be interrupted at any step. Sneakers, as described by Pottle and Green (1979b), tried to interfere on 5 occasions (out of 76 observed spawns), 4 of which spawns were interrupted by their arrival.

B. Juveniles

Small cunners displaying juvenile coloration (Johansen, 1925; Pottle, 1978; cf. also Fig. 5) were frequently seen in area 2, where topography and algae provided them

Figure 5. Territorial male cunner (above) and 'juvenile' cunners (under). One of these last fish released sperm when captured.

with shelter. Presumably because of lack of cover, they usually did not frequent areas 1 and 3.

The term 'juvenile' only refers to coloration and size (<100mm TL). One such juvenile was accidentally caught and it released sperm. On at least one occasion a 'juvenile' was seen to spawn with a female : he swam over her and the spawning rush immediately ensued without preliminary courtship.

Juveniles also attempted interference spawning and were vigorously chased by territorial males, a fact also reported by Pottle and Green (1979a). All chases performed on juveniles were of high intensity, often lasting for more than 5 seconds (as compared to an average of 2.4 seconds for other chases (Pottle and Green,1979b)) or until the pursued fish retreated under cover. Although small cunners were rarer in areas 1 and 3, they elicited the same strong response from resident males of those regions as well. Territorial males foraged sporadically in algal clumps where juveniles were known to be present from previous observations.

Food items

A. Feeding behaviors

1. Territorial males

Territorial males fed more in the morning and almost always on substrate organisms. Exceptions to this last fact were observed when ,in August, 1980, several jellyfish (Aurelia sp) floated over the territories. Some territorial males swam in the water column to take bites at these invertebrates. A resident male was often joined by other cunners which were then chased by him.

The feeding behavior of cunners on the benthos is conspicuous : the fish assumes a head down/tail up position and its lips are protracted, showing the teeth. A quick plucking movement follows as the fish feeds.

Food items thus taken could rarely be identified because either they were too small or because the fish had its snout under a rock or in an algal clump. Most of the prey which could be identified were ophiuroids.

2. Females and other males

Females and non-territorial males were easily attracted by bait throughout their entire active period. They also fed in the water column and on the benthos. This group was often seen to feed in the afternoon.

B. Alimentary tracts contents

The alimentary tracts contents of 38 territorial males were analysed : remains of urchins were present in all ; chitons, ophiuroids and limpets occurred in more than 60% of the alimentary tracts (Fig. 6). These results corroborate, on the whole, those of Martin (1979) who found urchins and limpets to be dominant food items. His findings were based on a sample of 15 as compared to 38 for the present study, which might help to explain the difference of diversity.

'Food item' is defined here as any type of invertebrate found in the alimentary tracts of territorial males . Most invertebrates from benthic samples taken in territories and corresponding to this criterion were used for correlations between food items and other variables. This choice did not necessarily reflect the content of the benthic samples

analysed. For example, Hiatella arctica, the arctic rock borer, dominated most of benthic samples in quantity but was not included in food items correlations. This bivalve lives under crustose algae, which makes it generally unavailable to cunners.

C. Benthic samples

The density per m of potential food items is shown for 9 territories in Table 7.

With the exception of chitons (TON5 (not shown) and TON10) and ophiuroids (OPHI010), all food items densities are negatively correlated with territory size (Table 8), which would suggest that larger territories are more likely to have lower densities of food. However the abundance of food items may remain comparable between territories. The same type of relationship holds for most of the correlations with the number of feedings.

Correlations between food items and depth are positive. This seems to be also the case for other sites in Conception Bay where the density of invertebrates increases with depth (Keats, pers. comm.).

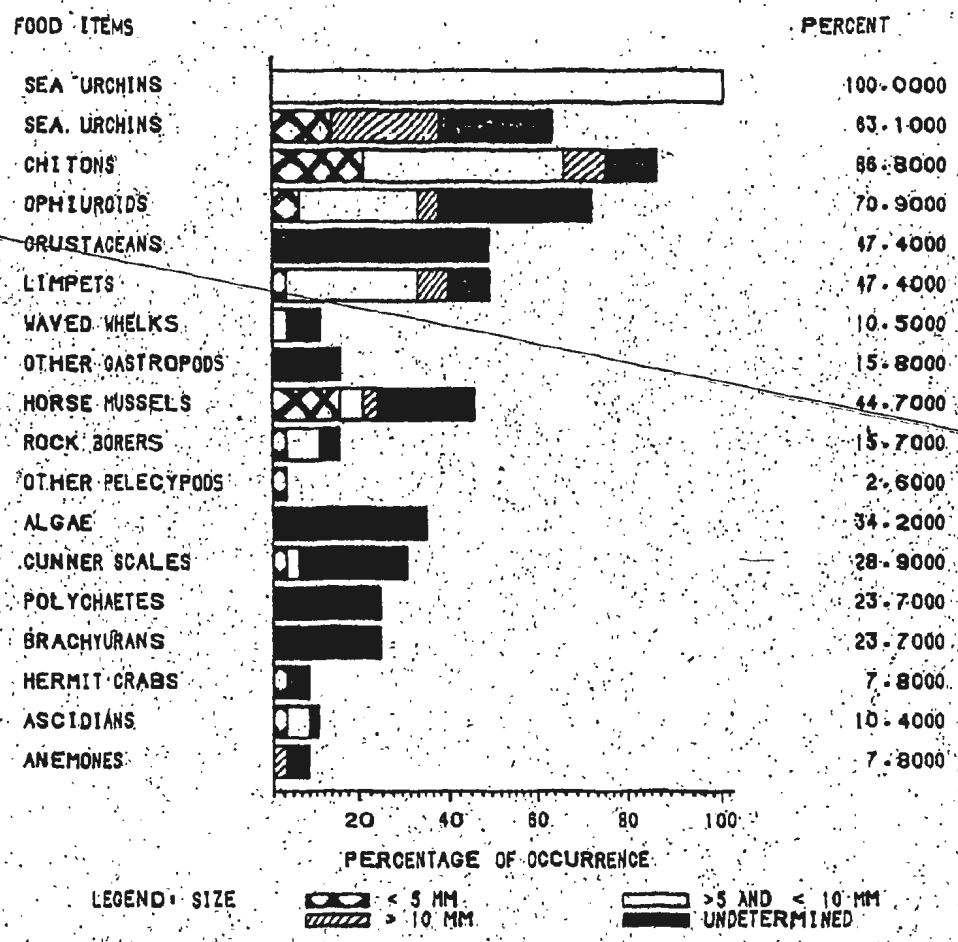


FIGURE 6. PERCENTAGE OF OCCURRENCE OF DIFFERENT FOOD ITEMS IN TERRITORIAL CUNNERS (*TAUTOGOLABRUS ADSPERSUS*) STOMACHS (N=38)

SEA URCHINS= *STRONGYLOCENTROTUS DROEBACHIENSIS*
CHITONS= *TONICELLA RUBRA*
WAVED WHELK= *BUCCINUM UNDATUM*
BRACHYURANS= *CANCER & HYAS SPP*
LIMPETS= *ACMAEA TESTUDINALIS*
HERMIT CRAB= *PAGURUS SP*
OPHIUROIDS= *OPHIOPHOLIS ACULRATA*
ARCTIC ROCK BORER= *HIATELLA ARCTICA*
HORSE MUSSELS= *MODIOLUS MODIOLUS*
ASCIDIANS= *HALOCYNTHIA & MOLGULA SPP*
CRUSTACEANS= CAPRELLIDS OR EUPHAUSIDS

Table 7. Densities (per m^2) of benthic food items in territories of some males *Tautogolabrus adspersus*, coupled with behavioral and physical parameters.

Male	Total Length (mm)	Territory size (m^2)	Spawns	Courtships	Feedings	Aggressions	Area	Mean depth (m)	Ton 5	Ton 10	Urch 5	Urch 10	Acma 10	Muss	Crus	Ophio 10	Polych
12	258	19.2	3	125	7	330	2	4.5	9.6	38.4	108.8	54.4	9.6	6.4	220.8	22.4	585.6
9	230	22.9	4	175	3	478	2	3.0	32.0	108.8	288.0	188.8	44.8	52.8	544.0	120.0	435.2
10	251	39.7	5	69	41	131	3	4.5	52.8	86.4	164.8	148.8	54.4	17.6	416.0	80.0	553.6
15	243	41.1	4	62	7	178	1	8.5	284.8	208.0	316.8	113.6	14.4	17.6	320.0	131.2	590.4
13	242	41.7	7	117	13	284	2	3.0	84.8	46.4	62.4	27.2	4.8	505.6	432.0	36.8	537.6
2	243	47.9	2	39	17	366	2	3.0	20.8	100.8	36.8	43.2	16.0	72.0	60.8	92.8	316.8
16	276	72.2	2	38	11	207	1	8.5	240.0	128.0	275.2	91.2	11.2	11.2	300.8	147.2	323.2
11	246	82.3	5	86	18	198	3	4.5	38.4	60.8	110.4	86.4	22.4	12.8	238.4	56.0	492.8
5	266	101.3	13	303	21	351	3	4.5	30.4	83.2	51.2	38.4	6.4	22.4	136.0	57.6	105.6

Ton 5 = *Tonicella rubra* < 5.0 mm

Ton 10 = *Tonicella rubra* ≥ 5.0 mm and < 10.0 mm

Urch 5 = *Strongylocentrotus droebachiensis* < 5.0 mm

Urch 10 = *S. droebachiensis* ≥ 5.0 mm and < 10.0 mm

Acma 10 = *Acmaea testudinalis* ≥ 5.0 mm and < 10.0 mm

Muss: *Mytilus edulis* and *Modiolus modiolus*

Crus: Crustaceans < 15.0 mm

Ophio 10 = *Ophiopholis aculeata* ≥ 5.0 mm and < 10.0 mm

Polych: various polychaetes

Table 8. Pearson correlation coefficients (1) between densities of food items per m2, (2) in male cunners territories and some physical and behavioral parameters. N = 9. Polych = polychaetes, TON10 = Tonicella rubra <10mm and >5mm, Ophio10 = Ophiopholis aculeata <10mm and >5mm, Urch5 = Strongylocentrotus droebachiensis <5mm, Urch10 = S. droebachiensis <10mm and >5mm, Crus = various crustaceans, Acma10 = Acmaea testidunalis <10mm and >5mm.

	Polych	TON10	Ophio10	Urch5	Urch10	Crus	Acma10	Feeding frequency	Depth
Territory size	-0.64*	0.19	0.23	-0.29	-0.27	-0.36	-0.28	0.57	0.30
Polych		-0.12	-0.11	0.44	0.36	0.52	0.35	-0.25	0.02
TON10			0.93***	0.53	0.52	0.02	0.31	-0.17	0.51
Ophio10				0.54	0.60*	0.09	0.45	-0.13	0.36
Urch5					0.84***	0.72**	0.48	-0.47	0.58*
Urch10						0.53	0.85***	-0.25	0.30
Crus							0.30	-0.31	0.13
Acma10								0.03	-0.08
Feeding frequency									0.01

(1) Values are Log10(X+1) transformed.

(2) Not all the food items are shown.

*P<0.1, **P<0.05, ***P<0.01, ****P<0.0001

D. Multiple regressions of food related parameters on territory size and feeding intensity

Multiple regressions were calculated for territory size and the number of feeding behaviors (Tables 9 and 10). The goal was to see if it was possible to develop a model which would take into account some variables and predict the outcome of others. The model was kept at its simplest to render the interpretation as realistic as possible. One problem was that many variables are highly correlated (Table 9) and such strong correlations can bias the model. This is why the choice of variables is a compromise between their reality and their degree of intercorrelation.

When only behavioral parameters are taken into account, the sole variable providing an 'insight' on territory size is the length of the fish (4% of the variance; Table 5, p.38). When food items are inserted into the model, it appears that density of polychaetes and depth together account for 51% of the variation between territories, not a very good fit.

A stepwise regression on the feeding intensity leads to better results (Table 10). Territory size alone is a good

Table 9. Stepwise regression of the variables (1) providing the best fit with territory size.

Variable entered(*)	Variance accounted for by variable(R2)	Total variance	Mean Square Error(MSE)	F (model)
Polychaetes	0.41	0.41	0.037	4.81
Mean depth of territories	0.10	0.51	0.036	3.08
Urchins <10mm	0.05	0.56	0.038(a)	2.12
Chitons <10mm	0.05	0.61	0.043	1.57
Total length of males	0.002	0.61	0.057	0.94

(1) Values are Log10(X+1) transformed.
(*) Order of inclusion based on Minimum R2 improvement.
(a) The entry of this variable and of the following does not contribute significantly to the fit of the model.

Table 10. Stepwise regression of the variables (1) providing the best fit with feeding intensity.

Variable entered(*)	Variance accounted for by variable(R2)	Total variance	Mean Square Error(MSE)	F (model)
Territory size	0.32	0.32	0.068	3.35
Aggression frequency	0.19(a)	0.19(a)	0.060	2.90
Urchins <5mm	0.33	0.82	0.021	13.85
Limpets <10mm	0.05	0.87	0.018	10.99
Total length of males	0.07	0.94	0.010	15.31
Territory size	0.01	0.95	0.011(b)	11.85
O. aculeata <10mm	0.00	0.95	0.017	6.59

(1) Values are Log10(X+1) transformed.

(*) Order of inclusion based on Minimum R2 improvement.

(a) Variance accounted for by Aggression frequency when considered as first variable entered. At the second step, Territory size is replaced by Aggression frequency which is complementary with Urchins: these two variables together provide the best two variables model, although Territory size alone gives the best fit for a one variable model.

(b) The entry of this variable and of the following does not contribute significantly to the fit of the model.

predictor of feeding intensity, accounting for 32% of the variation. However, when the model is increased to two variables, aggressivity and the density of urchins <5 mm account for the greatest variance (82%).

The food items which account for the greatest variance in feeding intensity (S. droebachiensis and A. testudinalis) according to the model, are also the same ones found most often by Martin (1979) in territorial cunners' alimentary tracts.

Relationship between territory size and food availability

A. General observations

The goal of the net experiment was to manipulate indirectly the food of territorial fish and to quantify the consequences as related to behavioral variables. It was believed that such consequences might be evident through changes in the frequency of feeding behaviors. As previously stated, this type of behavior is more frequently

observed in territorial males during the morning. Consequently, observations were made in the morning, after the spawning season. Throughout the whole period of observations, which was spread over almost a month (from mid-August to mid-September), no courtship was ever noted. During the duration of the experiment, water temperature varied irregularly from 15° C to 12° C. The behaviors observed were grouped into 3 categories : feedings (variable FEED), intraspecific aggressions (variable AGRESA) and interspecific aggressions (variable AGRESER).

After the first series of observations and before the installation of the nets, attempts (for the most part unsuccessful) were made to capture territorial males and to weigh them. One result was that the male which was supposed to act as a control became increasingly wary of divers. It came to a point that whenever a diver was less than 5 m away he would leave his territory. Consequently we had to switch to another male shortly after the observations on the nets began.

These observations started the day after the last net was installed. Reactions of the males to the nets were varied. The male whose territory was 100% covered left and was only sporadically seen over it thereafter. He usually

swam in mid-water. Two males (75% cover - large territory and 75% - small territory) did not seem to be affected and kept on patrolling as usual. Another (50% - small territory) was reluctant to pass over the net at first but gradually resumed patrolling over that portion of his territory after 2 days. He progressively extended his territorial area around and slightly over the area once occupied by the male with 100% cover. Finally, the 50% - large territory fish was never seen to go nearer than 3 m to the netted area of his territory.

Table 11 shows the quantified behaviors in terms of averages per day before and after installation of the nets : there is a decrease in the variables FEED and AGRESA . The variable AGRESER increases but because of the infrequency of its occurrences, its distribution is not normal nor is its variance homogeneous. Reference to this type of behavior will not therefore be made.

T-tests run on log-transformed data (Table 12) to ascertain if there is a difference between the means of behaviors before and after placement of the nets show that the decrease in AGRESA is significant ($P < 0.05$).

Table 11. Average number of behaviors observed per 30 minutes before and after installation of nets covering part of the food supplies of territorial males T. adspersus.

Fish	Territory area(m2)	% covered	Feedings (1)		Aggressions intra-specific (2)		Aggressions inter-specific (3)	
			Before	After	Before	After	Before	After
1	45.2	50	2.4	4.4	15.0	17.9	0.4	1.9
2	102.7	50	5.7	1.9	19.4	12.0	0.1	0.0
3	101.3	75	4.4	2.6	10.9	12.9	0.0	0.0
4	41.7	75	5.7	1.3	15.6	14.6	0.0	0.1
5	32.7	100	4.7	0.6	9.7	2.4	0.1	0.0
6	52.2	0	1.9		18.0		0.3	
7	36.3	0		3.4		4.2		0.0

(1) referred to as FEED in the text

(2) referred to as AGRESA in the text

(3) referred to as AGRESER in the text

Table 12. Results of T-tests between different behavioral variables (1) before and after installation of nets covering part of the food supplies of territorial males T. adspersus.

Variable	Mean before	Mean after	df	F	Significance
Feeding intensity	0.6890	0.4934	4	1.55	N.S.
Aggressions intra-specific	1.1863	0.9957	4	7.20	P<0.05
Aggressions inter-specific	0.0571	0.0840	4	9.53	P<0.03

(1) Values are Log10(X+1) transformed.

B. Influence of territory size.

The samples were too small to provide reliable data to detect differences with regard to territory size or percentage of covering.

Correlations between the variables were calculated before and after installation of the nets. The 0% covered area was not included because of the change of male. Those correlations and their differences in increase are shown in Table 13. The second largest change occurs in the correlation between AGRESA and FEED. The correlation between FEED and TERRITRY also increases.

When only the functional areas (i.e. the non-covered part) of territories are taken into account, the correlation FEED - TERRITRY increases even more (Table 14).

Morphometric data

Regressions of weight against length were calculated for territorial males as well as for non-territorial males

Table 13. Pearson correlation coefficients between physical and behavioral parameters (1) in territorial males T. adspersus before and after installation of nets covering part of their food supplies. B=before installation of nets, A=after inst. of nets, D=percentage of total possible variation.

		Aggressions inter-specific	Territory size	Aggressions intra-specific (2)
Feeding Intensity (3)	B	-0.86	0.23	0.13
	A	0.74	0.39	0.80
	D	80%	8%	33.5%
Aggressions inter-specific (4)	B		-0.27	0.20
	A		-0.29	0.45
	D		-1%	12.5%
Territory size (5)	B			0.57
	A			0.44
	D			6.5%

(1) values are Log10(X+1) transformed

(2) referred to as AGRESA in the text

(3) referred to as FEED in the text

(4) referred to as AGRESER in the text

(5) referred to as TERRITRY in the text

Table 14. Pearson correlation coefficients (1) between some variables in males T. adspersus after installation of nets covering part of their food supplies. Note : only the functional (non covered) area of the territories is considered in this table.

	Aggressions inter-specific (2)	Territory size	Aggressions intra-specific
Feeding intensity	0.59	0.77	0.48
Aggressions inter-specific		0.14	0.32
Territory size			0.20

(1) Values are Log10(X+1) transformed.

(2) cf. Table 13 for names used in the text.

and females caught in July and August, i.e. during the last weeks of or after the spawning season. After examination of the residuals, it was decided that log10 transformed values were most suitable.

Regression lines($P<.0001$) for all three groups are shown in Fig. 7 . ANOVAS on these data (Table 15) show that there is a significant difference ($P<.0001$) between the lengths of the members of the 3 groups and *a posteriori* tests indicate that territorial males are longer than females and non-territorial males ($P<.05$). The last two groups do not differ significantly. Territorial males are also heavier (Table 16).

An Ancova (Analysis of Covariance) run to test the dissimilarity of the regressions does not yield any significant result (Table 17). It is therefore probable that in August, the three behavioral groups have the same length-weight relationship.

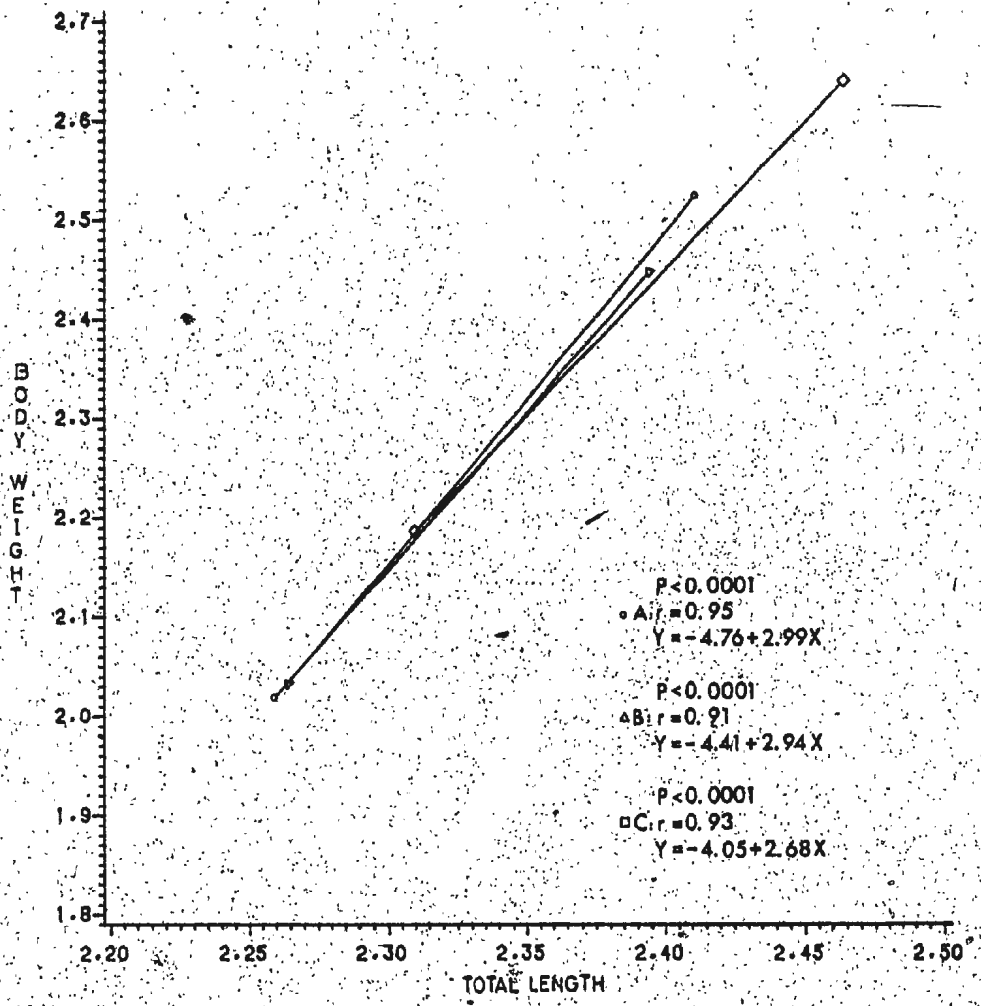


FIGURE 7. PREDICTED VALUES OF REGRESSIONS OF WEIGHT (IN G) VERSUS LENGTH (IN MM) IN DIFFERENT BEHAVIORAL GROUPS OF *TAUTOGOLABRUS ADSPERSUS* (FEMALES (A), NON-TERRITORIAL MALES (B), TERRITORIAL MALES (C))

FOR AUGUST

VALUES ARE LOG10(X+1) TRANSFORMED

Table 15. One-way anova of total length (1) of a sample of T. adspersus caught in August. Duncan's multiple range test is used as a posteriori test. Means with different letters are significantly (P<0.05) different.

Source of variation	df	Sum of squares	Mean square	F	P>F
Behavioral group	2	0.0523	0.0261	12.56	0.0001
Error	85	0.1770	0.0020		

Behavioral group	N	Mean (transformed)	Mean (non transformed)	Grouping
Territorial males	36	2.388	245.8 mm	A
Females	27	2.354	227.7 mm	B
Non-territorial males	25	2.329	214.6 mm	B

(1) Values are Log10(X+1) transformed, unless otherwise indicated.

Table 16. One-way anova of body weight (1) of a sample of T. adspersus caught in August. Duncan's multiple range test is used as a posteriori test. Means with different letters are siginificantly (P<0.05) different.

Source of variation	df	Sum of squares	Mean square	F	P>F
Behavioral group	2	0.3788	0.1894	9.81	0.0001
Error	85	1.6409	0.0193		

Behavioral group	N	Mean (transformed)	Mean (non transformed)	Grouping
Territorial males	36	2.367	244.3g	A
Females	27	2.291	208.3g	B
Non-territorial males	25	2.208	168.0g	C

(1) Values are Log10(X+1) transformed, unless otherwise indicated.

Table 17. Abridged ancova table of body weight versus total length (1), using this last variable as covariate. Sample of T.adspersus caught in August.

Ho	Source	SS	df	MS	F	Significance
The groups are sampled from populations of equal slopes	Variations among regressions	0.00325	2	0.00162	0.65	n.s.
	Error (average variation within regressions)	0.20492	82	0.00249		
Assuming that the groups share a common slope, they are sampled from the same population (i.e. there is a single regression for all groups).	Means of body weight adjusted for length	0.00590	2	0.00295	1.19	n.s.
	Error (deviation from a common slope)	0.20818	84	0.00247		

(1) Values are log10(x+1) transformed.

The same type of regression was done for the same behavioral groups captured in November. A major difference is in the number of territorial males (only 5). Regression lines ($P<.0001$ for non-territorial males and females; $P<.15$ for territorial males) are shown in Fig. 8. There are significant differences in length and weight among the groups (Tables 18 and 19).

An Ancova run on these data reveals that there is a significant difference among the regression lines (Table 20). The probability values associated with the regressions show that territorial males have a different length-weight relationship than non-territorial males and females. (Table 21). This indicates that at the same size, before entering torpid state, territorial males are actually lighter than females or non-territorial males.

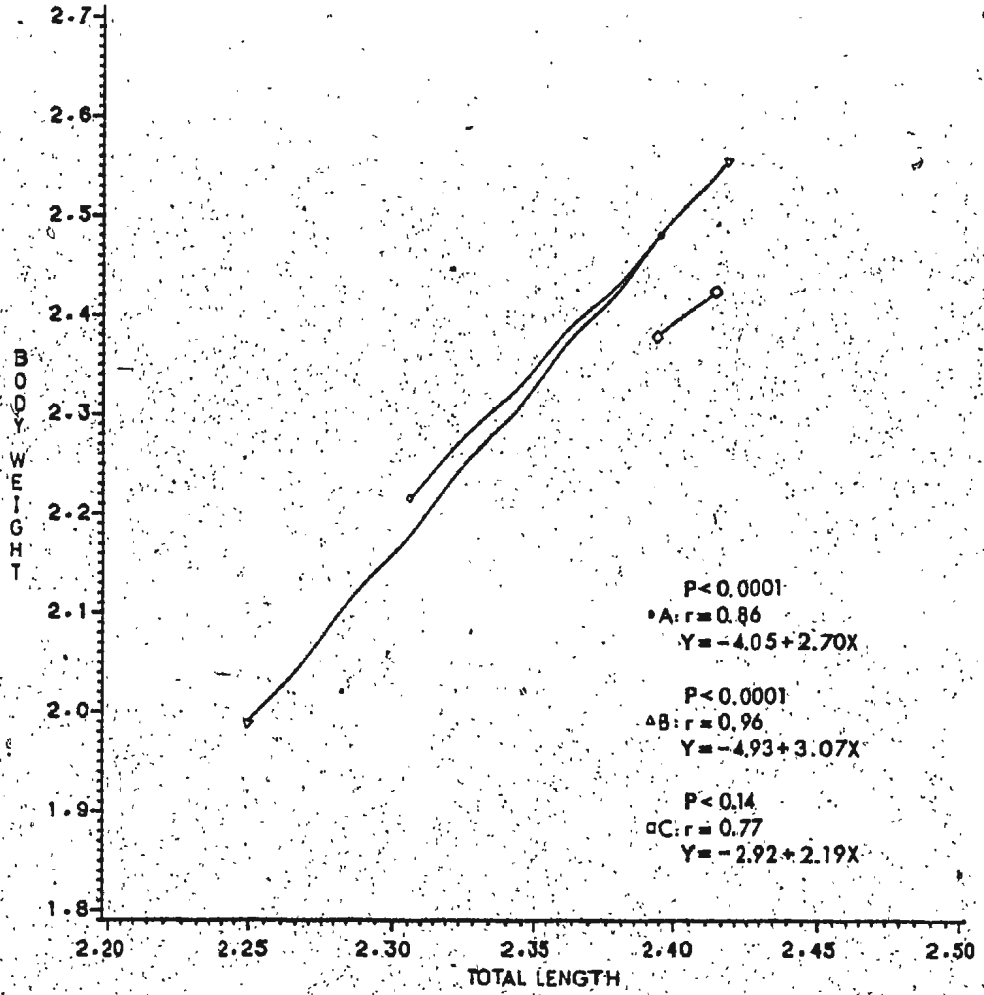


FIGURE 8 PREDICTED VALUES OF REGRESSIONS OF WEIGHT (IN g) VERSUS LENGTH (IN MM) IN DIFFERENT BEHAVIORAL GROUPS OF *TAUTOGOLABRUS ADSPERSUS* (FEMALES (A), NON-TERRITORIAL MALES (B), TERRITORIAL MALES (C))

FOR NOVEMBER

VALUES ARE LOG10(X+1) TRANSFORMED

Table 18. One-way anova of total length (1) of a sample of T. adspersus caught in November. Duncan's multiple range test is used as a posteriori test. Means with different letters are siginificantly (P<0.05) different.

Source of variation	df	Sum of squares	Mean square	F	P>F
Behavioral group	2	0.0210	0.0104	8.97	0.0004
Error	57	0.0666	0.0011		

Behavioral group	N	Mean (transformed)	Mean (non transformed)	Grouping
Territorial males	5	2.397	249.8mm	A
Non-territorial males	29	2.383	242.6mm	A
Females	26	2.348	223.7mm	B

(1) Values are Log10(X+1) transformed, unless otherwise indicated.

Table 19. One-way anova of body weight (1) of a sample of T. adspersus caught in November. Duncan's multiple range test is used as a posteriori test. Means with different letters are siginificantly (P<0.05) different.

Source of variation	df	Sum of squares	Mean square	F	P>F
Behavioral group	2	0.0993	0.0497	4.18	0.02
Error	57	0.6777	0.0118		

Behavioral group	N	Mean (transformed)	Mean (non transformed)	Grouping
Non-territorial males	29	2.391	253.8g	A
Territorial males	5	2.348	224.0g	A B
Females	26	2.305	207.5g	B

(1) Values are Log10(X+1) transformed, unless otherwise indicated.

Table 20. Abridged ancova table of body weight (1) versus total length, using this last variable as covariate. Sample of *T. adspersus* caught in November.

Ho	Source	SS	df	MS	F	Significance
The groups are sampled from populations of equal slopes	Variations among regressions	0.00272	2	0.00136	0.66	n.s.
	Error (average variation within regressions)	0.11138	54	0.00206		
Assuming that the groups share a common slope, they are sampled from the same population (i.e. there is a single regression for all groups).	Means of body weight adjusted for length	0.03646	2	0.01823	8.95	P<0.0004
	Error (deviation from a common slope)	0.11410	56	0.00203		

(1) Values are log10(x+1) transformed.

Table 21. A posteriori test comparing the body weight means of a sample of T. adspersus caught in November. The values of body weight are adjusted for total length. Means with different letters are significantly ($P<0.001$) different.

Behavioral group	Mean (non transformed)	Mean (transformed and adjusted for Length)	Grouping
Females	207.5g	2.367	A
Non-teritorial males	253.8g	2.350	A
Territorial males	224.0g	2.267	B

DISCUSSION

Female Choice

Field observations made in Conception Bay for two consecutive reproductive seasons indicate that there is a difference in number of spawns between territorial males of Tautogolabrus adspersus (Table 1, p.31). Similar results have been found for other territorial labrids (e.g. Pseudolabrus celidotus - Jones, 1981; Halichoeres garnoti - Robertson,1981) as well as for other fishes (e.g. Cottus bairdi - Brown,1981; Eupomacentrus partitus - Schmale, 1981). Male reproductive success has often been shown to vary more than female reproductive success throughout the animal kingdom (for references, see Trivers,1972).

Because females of most animals invest more energy in their gametes than males do, the former become the limiting sex (Williams,1975) and variations in male reproductive success are generally attributed to selective female choice. In order to protect her investment, a female should base her choice of mate on several criteria. Among cunners of Conception Bay, the possession of a territory is one of these criteria : all the observed spawns involved at least one territorial male.

To select a mate, a female can assess the potential partner in two ways : directly, in looking at some physical or behavioral features of the male itself, or indirectly by evaluating the quality or quantity of some of his possessions. These male characteristics must be, of course, variable and appraisable prior to mating (Searcy,1979). Male cunners can be evaluated through both ways, since the successful ones (successful relative to spawning) differ with regard to territory size and exhibit variations in physical and behavioral traits. Because of this, it is difficult to sort out the factors that lead a female cunner to breed with a particular male at a specific site : site quality and male quality are expected to evolve a positive relationship if there is any competition for favourite sites (Howard,1978).

Such competition seems to occur in Conception Bay. Pottle (1978) and Green (unpublished data) removed territorial male cunners from their sites and observed that the vacant territories were either soon annexed by adjacent territorial males or occupied by newcomers. This indicates that there is a floating population of males which find the acquisition of a territory advantageous enough to undertake fights and probable energy expenditures.

It is doubtful that territorial males energetically stand to gain from their property. In fact, they tend to be under the average population weight for their length in November, just before entering winter torpor (Tables 20 and 21, pp. 73 & 74). This physiologically disadvantageous condition could take a toll during the torpor the fish undergo in winter months. Olla et al. (1980) observed that big tautogs migrate during winter to deeper waters, where the occurrence of conditions inducing torpor in these fish is presumably irregular. They suggested that this could permit large tautogs to feed intermittently and to maintain a better overall condition so that energy reserves would be higher at the onset of the spawning season. Although possible, such migrations have not yet been observed in Conception Bay.

1. Territory quality

The reason a male cunner fights to acquire and keep a territory is that a territory increases his chances at reproduction.

Yet, what is attractive to a female in a territory? The site itself apparently is not too important : depth is not correlated to spawning success (R=-0.13) and the results of ANOVAs using depth or area as grouping variables are not significant with regard to the distribution of spawns. However, territory size is correlated to spawning success (R=0.56, P<0.05). Males with larger territories do tend to spawn more often. According to multiple regression analysis, differences in territory size account for 17% of the variation in number of spawns .

It is doubtful that females could be attracted by the food content of a territory : most of the correlations between spawn and food items are negative and, therefore, probably stem from the correlations between food and territory size (territory size is negatively correlated to most densities of food items). Also, females were more often chased in the morning, when territorial males spent more time feeding.

Female cunners are not restricted in their foraging areas, as territorial males are (*). They forage everywhere on the benthos and in the water column, and have access to a more diversified array of food than territorial males, as attested by alimentary tracts content analysis (Martin,1979). Because of the varied diet of the species (Anctil,1969; Chao, 1973; Olla et al.,1975) food is probably not an economically defendable resource in Conception Bay.

Although it may be safer for a female to evaluate her mate indirectly (Searcy,1979), since males can be deceptive about their own quality but not about the quality of their territories, territories do not seem to provide definitive criteria on which a female cunner could base her choice.

However, the physical characteristics of the environment of Broad Cove are not limiting for females : food is available at various locations, no nesting site is necessary, and most cunners, territorial and non-territorial ones, congregate at night in various shelter sites outside

(*) : Pottle and Green (1979b) noted the existence of some territorial females in Conception Bay, around the same study site. According to our observations, these females constitute an exception rather than a rule.

most territories. Therefore, the bulk of the variation in number of spawns has to stem from inter-individual physical or behavioral differences.

2. Male quality

When looking at the potential effect of some physical criteria in a species, one has to make sure that the animal under study can well perceive those same criteria. Territorial males are significantly longer than females and non-territorial males, but can this difference in size be assessed by cunners? Although I am not aware of any study on the perception of shapes by cunners, indirect evidence tends to confirm that these fish can perceive shapes, movements, and maybe even colors with accuracy. Vision, though often limited by turbidity, is probably the primary sense of most fish species dwelling in surface-lit waters (Fine et al., 1977). The cunner is a benthic feeder and like other fish which feed on benthos, its retina structure has the potential to differentiate quick movements and small objects (Anctil, 1969). Moreover, "many pelagic and casual benthic feeders rely almost exclusively on vision to locate food..." (Brawn, 1969 cited in Ware, 1973:301). Cunners have been observed in the field (Martin, 1979) and in the lab (Anctil, 1969) to have extensive eye movements.

It is, therefore, reasonable to assume that cunners can perceive differences in size among conspecifics. Size is often closely related to fecundity in fishes (Blaxter,1969). It can also indicate other qualities. For example, large male mottled sculpins (Cottus bairdi) make better egg guardians than smaller males and females show their preference accordingly (Brown,1981).

However, size (total length) is not correlated with spawning success in cunners (R=-0.03, Table 2, p.33). Since territorial males are longer than the two other behavioral groups, and territorial males are about the only ones observed to spawn, the size of a cunner probably plays an indirect role in mating success. Males have to attain a certain size to become serious contenders for territories. If mating success is limited to a certain class, one would expect the small males to put everything they have into growth to attain a competitive size as soon as possible. Another strategy common in labrids is to begin life as female, to spawn as such until a certain size is reached where competition for territories is feasible and then to become a male (Warner and Robertson,1978). This strategy, termed protogynous hermaphroditism, has not been confirmed in the cunner (Pottle,1978). A possible restraint to it could be the winter torpor coupled with the high physiological costs involved in the transformation. Labrids

of warmer seas are active throughout the year, which presumably helps to support the physiological cost. It has to be born in mind that, as Warner (1978:87) wrote, "the existence of hypothetical selection pressure for a trait in no way guarantees its appearance".

The previous hypothesis accounting for the presumed absence of protogynous hermaphroditism assumes that non-territorial males are not successful at spawning. This is not entirely true : interference spawning, in which another male rushes in to join a male and a female at the apex of their spawn, has been observed on some occasions in Broad Cove (Pottle and Green, 1979b; Martel, unpublished data). Obviously, the number of gametes thus fertilized is enough to perpetuate the tactic. Warner (1975) hypothesized that in a population where young males obtain a certain reproductive success, their fecundity at early ages may be high enough to minimize selection pressures for changing sex. Streaking (interference spawning) is mainly performed by small males of juvenile coloration (cf. Fig. 5, p.45). Their small size enables them to hide in algal clumps and narrow crevices inaccessible to territorial males.

Cunners spawn at a relatively low rate (an average of less than one spawn per hour, according to our observations) compared to tropical labrids (up to eight per hour -

Jones,1981) and their reproductive season is short (some labrids spawn throughout the entire year - Warner and Robertson,1978). Therefore, each spawning has a high relative value for male cunners as compared to other labrids. Males of a species with a low spawning rate are expected to expend more effort trying to detect small males (potential streakers (*)). They also have more time to devote to this than males with a higher spawning rate (Robertson,1978). Judging from the relative intensity of the chases involving territorial males and 'juveniles', this is probably the case for cunners. Female labrids have been shown to be reluctant to spawn when many potential interfering males were present (Warner and Hoffman, 1980).

For this last reason, the aggressiveness displayed by a male could provide a cue to females. It is sufficiently strong in certain males to cause them to break a spawning rush to chase an intruder. Labeled "aggressive neglect" (Hutchinson and MacArthur,1959), this behavior occurs when time taken for defense takes precedence over the courtship of females (Warner and Hoffman, 1980). For it to have evolved, the relative value of each spawn must be quite high.

(*) A streaker is defined as " a fish rushing in to join a male and a female at the climax of pair spawning." (Warner and Robertson, 1978:21).

Although aggression is weakly correlated with spawning success. ($R=0.33$, not significant) and accounts for only 5% of the variation in numbers of spawnings, it is strongly correlated with courtship intensity ($R=0.67$, $P<0.01$). This can be partially explained by the fact that many approaches (a component of aggressiveness) were directed towards females. It may also reflect the rate of intrusions into a territory. But then one has to ask why there are many or few intrusions in a particular territory : because of the site or of the owner?

Courtship intensity is highly correlated to reproductive success ($R=0.80$, $P<0.001$) . Again, this may reflect the frequency of female intrusions. It is advantageous for a male in a promiscuous species to have a low threshold of responsiveness to females. Such behavior can maximize the number of females he attracts, encounters and attempts to spawn with (Selander,1972). A high responsiveness will often result in males attempting to mate with females independently of the females' behavior (e.g. Trivers,1972), which is the case for male cunners. There is little advantage for a male to conceal low reproductive powers. Therefore, a correlation between courtship intensity and sperm level can be expected (Trivers,1972).

This may be one of the reasons why female cunner choice is correlated with courtship intensity. In courting intensely, a male is communicating to the female that he is willing to transfer sperm and that he has sufficient supplies of it, which is important since his sperm may have to compete with that of a streaker.

Willingness to mate is correlated with high levels of aggression in many animals (Wilson, 1981). In the cunner, this is further emphasized by the absence of correlation between number of aggressions and territory size (Table 2, p. 33). I suggest that in the cunner, aggressiveness and courtship intensity are both correlated with the reproductive state (aggression lasts throughout all the active months and relates also to ultimate goals). According to this hypothesis, cunner intra-specific aggression should peak during the spawning season, a phenomenon already described in at least two other labrids (Pseudolabrus celidotus - Jones, 1981 and Coris dorsomaculata - Tribble, 1982).

Male cunners execute a kind of post-spawning display, in the form of a strong arch, while descending to the substrate after a successful spawn. This display is essentially a more vertical version of the courtship

behavior. It is highly visible and observers could tell several meters away that a spawn had occurred. To the best of my knowledge, post-spawning display in labrids has only been described for Coris dorsomaculata (Tribble,1982). Tribble suggests that this type of display could attract females or demonstrate male reproductive success. Because of the visibility of the action, the same might hold for the cunner. It is probably advantageous for a male to display his successes. It is interesting to note that such behavior never attracted any small males, as did the spawning rush.

There are many intercorrelated factors pertaining to spawning success. Thus it is hard, without precise experiments to isolate these factors, to come up with a definitive answer with regard to female mating choice. When such experiments are done, an optimal solution is almost always looked for (see Pyke et al.,1977 and Davies,1978). However, in nature, problems tend to arise more at the same time instead of one after another and thus natural selection should favor compromises, resulting in the best mix of solutions rather than in one optimal solution (Janetos and Cole,1981).

Typically, the female cunner leaves its aggregation towards mid-afternoon and swims over the areas where the male territories are. She has been courted a few times when

in the group, but in general has not responded (no spawning was ever observed to take place in one of these aggregations). Once she is over the territorial grounds, she wanders around, feeding but mainly swimming. She is courted by almost all the territorial males she encounters. Some of them are more 'persistent' than others and they are the ones which stand the most chances to spawn (differences in courtship intensity are responsible for 52% of the variation of spawning success).

Also, territory size plays a role. But here the territory has to be seen just as a surface : since males do not cross their borders and females do, the physical contact of a particular male with a female is limited by the area he defends. If a female usually swims at a constant speed, the larger the area she is in, the longer the resident male will keep contact with her and the better his chances at spawning become.

The females can be influenced by the aggressiveness and the length (size) of the males. For the former, degrees of aggression and of courtship have been shown to be closely correlated, so it could be that females are evaluating the 'stamina' of males through aggressiveness. Another explanation could be that females attract other males, territorial and non-territorial, and these are chased by

residents for territorial trespassing. As for the length, territorial males might be more conspicuous or look more impressive, but the importance of this trait in spawning is minimal. It could be more important in determining the outcome of altercations generated when establishing a territory.

Territory Size

Advantages of territoriality must relate either to benefits deriving from maintaining large interindividual distances or to resources provided by the site (Brown and Orians, 1970).

Territoriality in male cunners fulfills both functions: since the acquisition of a territory is an essential prerequisite to successful spawning, reproduction is the ultimate benefit derived from the first function. The proximate goal (second function) must be maintenance, for territorial males feed exclusively within their borders.

Territory size can be determined by several factors, among which are the size and the energy requirements of the owner, his mobility, his behavioral characteristics and the density of competitors. Most of the models dealing with territory size take into account energy needs, food production and competitor density (e.g. Schoener,1971; Covich, 1976; Dill,1978; Hixon,1980).

1. Relation with food

Tautogolabrus is a benthic feeder eating mainly sessile prey, so it is possible to quantify potential food items. These tend to increase with depth, although there is no significant correlation with depth (an exception is urchins smaller than 5 mm). Indirect evidence for the importance of food with regard to territory size is provided by the fact that the number of feedings is significantly greater in area 3 (closest to shore) than in area 2 (the shallowest) and that territories in area 3 are significantly larger than in area 2 (Table 4, p.37). If feeding rate (number of feedings) varied proportionally with the abundance of food items (which are positively correlated with depth - Table 8, p.51), the number of feeding behaviors should be greater in area 1 than in area 3, which is not the case (Tables 1 and 4, pp. 31 & 37).

However, the distribution of food items inside particular territories was not investigated. Area 2 has many large boulders, crevices and algal clumps. Those clumps and crevices presumably provide an attractive habitat for small invertebrates. Also the crustose algae Lithothamnion glaciale is abundant along the sides of large boulders and with it is associated a dense fauna of polychaetes, bivalves and ophiuroids. In contrast, areas 1 and 3 are almost bare of relief and vegetation. Food items are likely to be more evenly dispersed where the relief is uniform.

With food items being concentrated, food requirements can be attained faster, necessitating less foraging (Schoener, 1971), hence territories of smaller size. A fish in area 3 would have to forage for longer and feed more often (because of the energy spent in longer foraging periods) than in area 2.

The importance of food in influencing territory size is further emphasized by the nets experiments. In some coral reef fishes, territory area has been demonstrated to vary proportionally with the owner's diet overlap with the intruders' (Myrberg and Thresher, 1974; Mahoney, 1981), the largest area being defended against conspecifics (100% diet overlap). If this is the case for the cunner, we should

expect manipulation of the food content of territories to most affect the rate of intraspecific aggression.

When the whole territory was covered by nets, the resident male left. For the fish with partially covered territories, the correlation between number of feedings and intraspecific aggressions increased dramatically when the cover was installed.

If there are food clumps in small territories (area 2) and a more even distribution in larger ones (areas 1 and 3), the effect of the nets is potentially more detrimental on the smaller. However the nets can 'miss' the patches and leave the occupant unaffected.(*)

The experiment was done with too few samples to be statistically significant, but the increased correlation between number of feedings and intraspecific aggressions makes sense in the context where food clumps would have been covered in area 2. That is, if the food suddenly becomes limited (its access being cut by the nets), a territorial male will have more food to eat if he keeps conspecifics out of his territory. Superficial examination (i.e. without

(*) : This element of chance infiltrated because according to previous observations, it was believed that the fish fed 'homogeneously', i.e. all over their own territories.

statistical test) reveals that the correlation between number of feeding behaviors and intra-specific aggressions is strongest in area 2 and weakest in area 3.

The experimental manipulation of resources which could be monopolized through territoriality has been reported in only three cases for fishes (Slaney and Northcote, 1974; Syrop, 1974; Hixon, 1981). In all instances the manipulation of food supplies resulted in changes in territory size consistent with the food defense hypothesis. Although the present experiment was not conducted for sufficiently long to show any significant change in territory area (aside from the 100% covered territory whose owner left), the reaction of the cunners is consistent with the food defense hypothesis.

Overall, the densities of food items are inversely correlated to male cunners' territory size . Such a relationship has previously been found in territorial fish (Ebersole, 1980), birds (Miller, and Watson, 1978), lizards (Simon, 1975), and marine gastropods (Stimson, 1973). Among cunners, large territories tend to have relatively low food densities. The term 'food' has a broad sense when applied to the cunner : the fish eats a variety of molluscs, crustaceans and echinoderms (Chao, 1973; Olla et al., 1975; Martin, 1979). Alimentary tracts contents of cunners taken

in Conception Bay may reflect more availability of prey than selection of particular items. No field or laboratory experiment has so far been done to determine if some food items are preferentially eaten when cunners are given the choice. This is why it is hard to explain variations in territory size through the presence or absence of particular food items. In the multiple regression on territory size, polychaetes appear to be responsible for 41% of the variation in territory size. These invertebrates were found mostly under crustose algae, where it is doubtful they are accessible to cunners. However, their weak representation in alimentary tracts contents does not necessarily mean that they are rarely eaten. Most of the food items found in alimentary tracts of cunners are calcareous components and a soft worm would presumably be quickly digested.

The multiple regression on the number of feedings gives better results. The food items which statistically explain the largest part of the variance in number of observed feeding behaviors are urchins smaller than 5 mm in diameter and limpets (Acmaea testudinalis), results which corroborate those of Martin (1979), who found that territorial males fed more on S. droebachiensis and A. testudinalis than did females or non-territorial males.

However the correlations found in the present study between food items and feeding intensity are negative (Table 8, p.51). Martin (1979) hypothesized that territorial males might selectively feed on A. testudinalis and S. droebachiensis. According to our data, the higher the density of these food items the lower the feeding rate of territorial males . Therefore, since sea urchins and limpets account for most of the variance in feeding intensity, it could be that 1) territorial cunners do not like these prey items, which is unlikely according to Martin's results, or 2) that these two prey items are energetically better and that a fish can eat proportionally fewer limpets and urchins and still meet certain physiological requirements. To test this last hypothesis, more data are needed on the type of foraging of territorial males as well as on the energetic value of the available prey items.

Another hypothesis to account for the negative correlation between cunner feeding and denaities of urchins and limpets would be that this is in fact a measure of the effect of cunner grazing on these invertebrates. Unfortunately, our data do not enable us to go further along this line. In that regard, more detailed experiments are necessary involving urchins, limpets and cunners .

Olla et al.(1981) surmised that territoriality in cunners is influenced by food distribution and abundance. While food is certainly important in a territory, our data tend to confirm Pottle and Green's (1979b) conclusion that territoriality is above all related to spawning.

Following Olla's reasoning, a territory and consequently the exclusive use of some food resource, would enable a territorial male to grow larger and maybe faster than non-territorial conspecifics. Female choice would then be related to male size (territorial males are larger than non-territorial ones). But our data show that spawning success is not related to male size. Moreover, some non-territorial males are larger than some territorial ones and spawning was never observed to occur in non-territorial fish aggregations.

2. Defendability

An important criterion in territory size is its defendability (Brown,1964; Davies,1978). A territorial animal can communicate its presence to others via, for example, chemical signals (such as in mammals - Wilson, 1981), auditory signals (birds - Peek,1972) or visual signals (birds,fishes - Peek,1972; Wilson, 1981).

Vision is probably a very important sense for the cunner. Our observations suggest that territorial males oriented themselves towards other fish mainly through vision. They did not show any reaction to fish which were a few cm away but out of their visual field, for example, hidden by a boulder.

Warner and Hoffman (1980) demonstrated that in some labrids, population density strongly affected the economic defendability of mating territories. After experimentally increasing the density of initial phase males (the equivalent of 'juveniles' in the cunner), they observed a decrease in territorial males' mating success. Their main study species, Thalassoma bifasciatum, held temporary mating sites (the same each day) and no reference was made to visual obstructions in territories. Presumably due to the high numbers of individuals, this was not judged important in territorial defendability. (They also did not mention any variation in territory size.)

According to our observations, this visual aspect is very important in the economic defendability of cunners' territories. Area 2 contains the smallest territories. It is also where the relief is the most variable, with large boulders (1.5m and more), algal clumps, ridges and

crevices. Furthermore, these also provide shelter to small cunners, responsible for most of interference spawnings.

Optimality theory (Schoener,1971; Pyke,1977) states that the basic life history strategies (feeding, reproduction) in animals take into account costs and benefits. It is unlikely that the animal itself is conscious of the ultimate costs and benefits derived from its action. He performs some actions because natural selection selected him to do so, by giving individuals who were using a certain strategy better reproductive success than those who were not and thus perpetuating the genes of the former.

For a territorial cunner, the benefits of holding a territory are reproduction (ultimate) and maintenance (proximate). Most of the costs of territoriality are related to energy expended to defend the area of exclusive use. In order to maintain a good balance between aggressive interactions and mating activities, a male has to be able to see intruders from a certain distance to keep them out. In area 2, where obstacles to visibility and shelter sites are numerous, this optimal distance is reduced. A fish who would attempt to hold a large territory in area 2 would probably increase its energy costs and alter the balance between costs and benefits. In areas 1 and 3, where the

substrate is flatter, the only serious limit to vision is water turbidity. Of course, even in crystal clear water, there is an upper limit set to territorial area by the energy costs involved in patrolling and repelling intruders. And again, a cunner territory must sustain its owner - there were no territorial males over sandy bottoms, although vision was probably maximal there.

Experimental manipulations to assess the importance of visual interference in the determination of territory size are realizable in the field and should confirm or disprove the preceding discussion.

Peregrinations

An unexpected question raised by this study concerns the adaptive significance of the 'peregrinations' done by territorial males .

In all observed cases, territorial males suddenly left their territory and went directly to one of the two known overwintering sites. The only visible social interactions were performed when the 'wanderer' passed over territories of other males . A similar type of behavior has been described for pomacentrids (see Sale,1978). Termed 'visiting', this behavior involving few agonistic displays, was, however observed to occur at its peak intensity just before and in the middle of the breeding season. Keenleyside (1972) suggested that two of the functions of visiting (or clustering, as he called it) could be to distribute information about reproduction and to help synchronize reproductive activity (Sale,1978).

Because its occurrence in the cunner is well after the spawning season, it seems doubtful that it is related to reproduction. But it could well help the fish synchronize the onset of their overwintering season, assuming that there

is any advantage for the individuals in doing so. This is purely hypothetical, but the fact that cunners form dense aggregations after and before entering into the substrate lends support to this proposition.

Peregrinations were observed for only one season, because of their late date of occurrence. Consequently the preceding discussion is based on irregular observations and planned examinations are needed to substantiate it.

CONCLUSIONS

1. There is differential spawning success between territorial male Tautogolabrus adspersus, spawning success being defined as number of spawns observed in a given period of time.

2. This differential spawning success is best explained by differences in male characteristics rather than by differences in characteristics of their territory.

3. However, territorial space is vital to the cunner and territory qualities cannot be entirely separated from owner qualities.

4. The ultimate function of a cunner territory is reproduction; the proximate one is maintenance.

5. Territory size is a function of

a) the relief of the area, which influences the visibility and consequently the defence of the territory. This assumes that cunners rely principally on vision to detect other fish.

b) food quantity and its distribution within the territory.

6. A new type of behavior, termed 'peregrination', was observed in territorial males. Its function could be related to overwintering, but no quantitative data are presently available to support or invalidate the hypothesis.

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Appendix

Pearson correlation coefficients (1) between behavioral and physical parameters of territorial males *Tautogolabrus adspersus* in Conception Bay in 1980 and 1981. In each case, N = 8, except for the correlations involving total length in 1980, where N=7.

		# of spawns	Feeding frequency	Courtship frequency	Aggression frequency	Mean depth of territories	Total length of males
Territory size	1980 :	0.46	0.41	0.12	-.032	0.56	0.37
	1981 :	0.59	0.51	0.17	-0.35	0.11	0.31
# of spawns	1980 :		0.22	0.77*	0.13	-0.009	-0.69
	1981 :		0.02	0.76*	0.20	-0.19	0.47
Feeding frequency	1980 :			-0.29	-0.80*	0.09	0.32
	1981 :			-0.34	-0.23	0.54	0.37
Courtship frequency	1980 :				0.65	-0.18	-0.74
	1981 :				0.66	-0.49	0.44
Aggression frequency	1980 :					-0.43	-0.39
	1981 :					-0.63	0.05
Mean depth of territory	1980 :						0.65
	1981 :						0.36

(1) Values are Log10(X+1) transformed.

* P<0.05